

ARCHITECTURE OF THE UPPER CARBONIFEROUS PTERIDOSPERM FROND *MACRONEUROPTERIS* *MACROPHYLLA*

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ABSTRACT. This paper presents the first full morphological description of *Macroneuropteris macrophylla*, the type species of its genus. The fronds are very similar in size to the more widely distributed *Neuropteris*, but are significantly less divided; the *M. macrophylla* pinnules are homologous to segmented, tertiary pinnae in *Neuropteris*. *M. macrophylla* is known only from westernmost Europe and easternmost North America.

It is now well established that many of the fern-like frond fragments found in the Upper Carboniferous of the palaeoequatorial belt are in fact the remains of seed-bearing plants, sometimes referred to informally as pteridosperms or seed-ferns. Being normally found in a fragmentary condition and without fertile structures, the classification of these fronds has posed serious problems. In recent years, however, attempts have been made to produce a more natural classification by using details of the frond architecture (i.e. the pattern of branching within the frond) and, more recently, epidermal structure.

The genus *Macroneuropteris* was erected by Cleal *et al.* (1990) as part of a taxonomic revision of one of these groups of pteridosperm fronds, previously assigned to *Neuropteris* (Brongniart) Sternberg. Laveine (1967, p. 80) had noted earlier that some species of *Neuropteris sensu lato* have less divided fronds and larger pinnules, referring to the group as the *Neuropteris* 'macrophylliens'. Laveine (1967, p. 314) maintained that these differences in frond architecture could largely justify the creation of a new genus, but was reluctant to make a formal taxonomic change, because of the possible disadvantages of splitting an apparently continuous evolutionary lineage. However, this stance was based exclusively on gross morphology. The cuticular evidence, such as that presented by Barthel (1961) and Cleal and Zodrow (1989), added weight to the argument for the generic separation of *Macroneuropteris*. The gross morphology nevertheless remains a key feature for understanding these fronds, and this has never previously been the subject of a detailed published investigation. The present paper therefore presents the first detailed description of the frond architecture of the type species, *Macroneuropteris macrophylla* (Brongniart) Cleal, Shute and Zodrow.

MATERIALS AND METHODS

The description is based on eight specimens in the palaeontological collections of The Natural History Museum, London, accession numbers V.3073 and V.63414–V.63419. Their provenance is stated as 'Coal Measures, Radstock, Somerset'. They probably originated from the Radstock Formation, and are thus late Westphalian D in age (*Dicksonites plueckenetii* Subzone *sensu* Cleal 1991; Cleal and Thomas 1994). All but V.63419 are stated to have been presented to the museum in the 1880s by Mr J. McMurtrie, a nineteenth-century geologist well known for his work on this coalfield (e.g. McMurtrie 1867, 1890, 1901). One of the specimens (V.63417) has been previously figured by Crookall (1959, pl. 42, fig. 3).

The specimens required no preparation, and were photographed using plane- or cross-polar illumination. Outline tracings were taken from the photographs, and then rescaled to a uniform magnification. These tracings are the basis of Text-figures 1–2. Plant macrofossils from the Bristol–Somerset Coalfield are unsuitable for cuticle work, but the epidermal structures of this species have been described previously by Cleal and Zodrow (1989), based on Canadian material.

The cuticular evidence described in these studies has been annexed to the emended diagnoses given in the systematic palaeontology section below.

Terminology for frond architecture follows that used by Cleal and Shute (1991). For the sake of simplicity, the terms 'upper' and 'lower' have been used instead of 'distal' and 'proximal' in the descriptions when referring to position in a frond segment. The term pinnule is used in its now widely accepted sense (e.g. Tryon 1960; Taylor and Taylor 1993; Niklas 1993) for the ultimate segment of the frond, irrespective of the order that the segment is within the frond.

DESCRIPTION

The specimens dealt with in this study fall into three broad groups: (1) wide rachises with broad, ovoid pinnules attached (V.63416(b), V.3073); (2) wide, dichotomous rachises (V.63416(a) and possibly V.63418); and (3) pinnate foliage with mainly elongate, linguaeform to subfalcate pinnules (V.63414, V.63415, V.63417, V.63419). These are taken to be the lower, middle and upper regions, respectively, of a bipartite frond. Some of the dimensions of these specimens are summarized in Table 1.

TABLE 1. Main dimensions of *Macroneuropteris macrophylla* frond fragments (in mm).

| Specimen no. | Primary width | Maximum primary rachis branch width | Secondary rachis spacing (outer/inner) ¹ | Secondary rachis offset ² | Maximum pinnule length |
|--------------|---------------|-------------------------------------|---|--------------------------------------|------------------------|
| V.63417 | — | 10 | 90/90 | 50 | 45 |
| V.63415 | — | 10 | —/— | — | 45 |
| V.63419(b) | — | 9 | 90/— | — | 60 |
| V.63418 | — | 8 | 90/90 | 70 | 45 |
| V.63414 | — | 8 | 90/100 | 50 | 50 |
| V.63416(b) | 16 | — | —/— | — | — |
| V.63419(a) | — | 4 | 100/— | — | 55 |
| V.63416(a) | 7 | 4 | 40/40 | 21 | 22 |
| V.3073 | 9 | — | —/— | — | — |

All measurements in millimetres.

¹ Refers to spacing on the outward and inward facing sides of the primary rachis branch.

² Refers to the distance between a secondary rachis on the outward facing side of the primary rachis branch, and the next, higher secondary rachis on the inward facing side of the primary rachis branch.

As these specimens were collected over 100 years ago, it is impossible to place the fossils in any sedimentological context, other than to state that they are preserved in a mudstone, possibly representing a flood-basin deposit.

Lower part of frond

The lowest preserved part of the frond is shown in V.3073 and V.63416(b) (Pl. 1; Pl. 2, fig. 3; Text-fig. 1C–D). Primary rachises, up to 190 mm long and 7–9 mm wide, have large pinnules alternately

EXPLANATION OF PLATE I

Macroneuropteris macrophylla (Brongniart) Cleal *et al.* V.63416; two frond fragments, one of a primary rachis below the main dichotomy of the frond, the other of the main dichotomy; photographed using cross-polarized reflected light; Radstock, Somerset, UK; upper Westphalian D; $\times 1$.



or sub-oppositely arranged. Pinnule spacing on either side of the rachises is 25–33 mm, and the ratio of pinnule spacing to rachis width is *c.* 2.5. Neither specimen shows the primary rachis attached to a cauline axis.

This part of the frond is also shown by the specimen figured by Kidston (1888, pl. 21, fig. 2). This shows a 135 mm length of primary rachis which is only 5 mm wide. The attached pinnules are arranged oppositely along the rachis at intervals of 15–16 mm; the ratio of pinnule spacing to rachis width is thus slightly higher (3.0–3.2) than in the specimens figured here.

Dichotomy of primary rachis

At least 190 mm from the point of attachment to the stem, the primary rachis underwent a dichotomy to produce two primary rachis branches. This dichotomy is clearly seen in V.63416(a) (Pl. 1; Text-fig. 1B). From the dimensions of the rachises and of the attached pinnules, it is apparent that V.63416(a) was part of a much smaller frond than that represented by most of the other specimens dealt with in this study. Such a small frond may have originated from near the top of a plant, or is perhaps the leaf of a small, juvenile plant. Whichever is correct, there is no reason to believe that the architecture of this small frond was significantly different from that of the larger fronds.

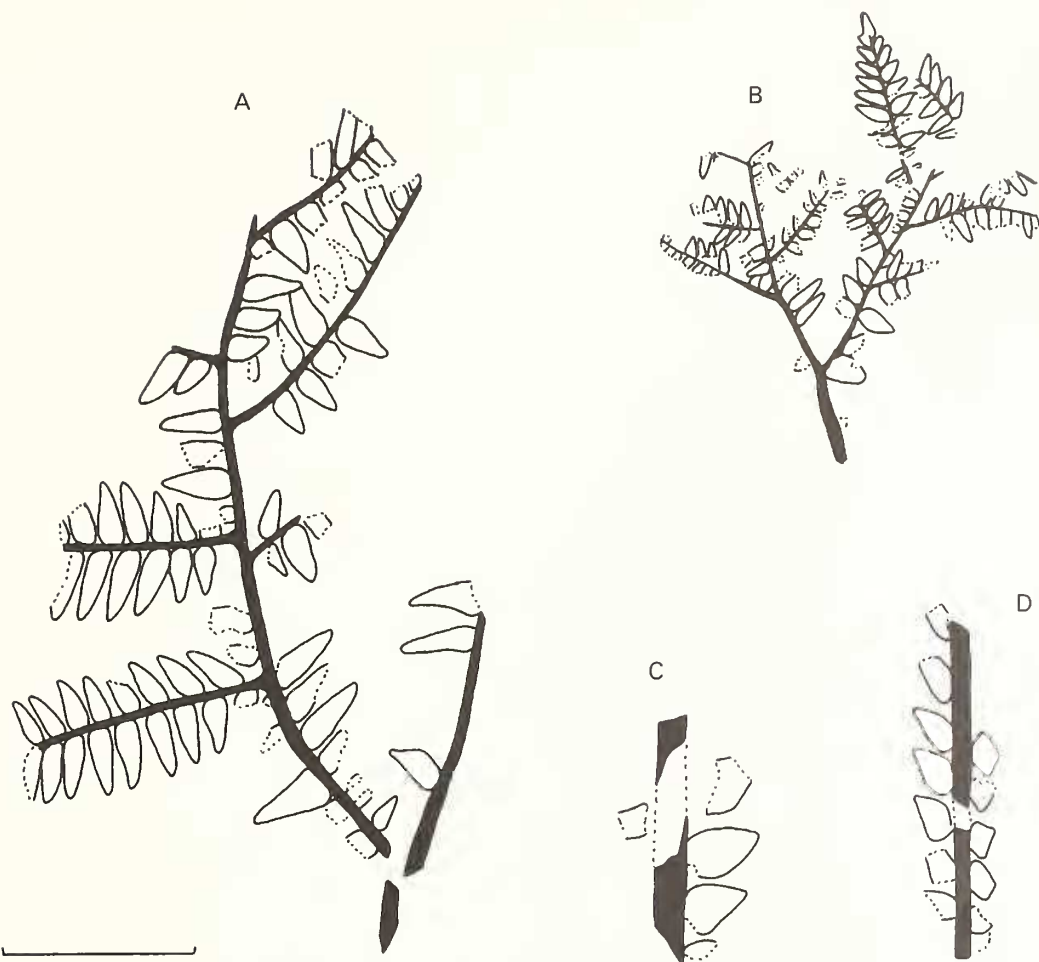
In V.63416(a), the primary rachis branches lie at 45° to one another, but there was probably some taphonomic distortion and this angle may have been wider in life. This distortion is most clearly seen in the left-hand primary rachis branch. If the angle between the primary rachis and the right-hand branch is about what it was in life, then the angle of the main frond dichotomy would be *c.* 70°. A narrower angle would cause the secondary rachises to overlap significantly in the middle of the frond, reducing the photosynthetic efficiency of the frond, and thus seems a less likely configuration. A similar situation arises with the specimen figured by Kidston (1888, pl. 21, fig. 2); the primary rachis branches are preserved at an angle of about 40° to one another, but in this case the right-hand branch has clearly been bent towards the centre of the frond. If the left-hand branch is taken to provide a better indication of the angle, then a value of about 65° is obtained for this dichotomy.

A similar angle of dichotomy of about 70° may occur in *Macroneuropteris scheuchzeri* (Laveine and Brousmiche 1982), as well as in other bipartite trigonocarpalean (medullosan) fronds (e.g. *Neuropteris*, *Odontopteris*, *Callipteridium* and *Margaritopteris*; Zeiller 1900; Potonié 1903; Laveine *et al.* 1977; Wendel 1980; Zodrow and Cleal 1988; Cleal and Shute 1991). One specimen (V.63418; Text-fig. 1A) appears to show a somewhat narrower angle of 55–60°, but there is again clearly some taphonomic distortion here. Nevertheless, some variation in the angle of the main dichotomy has been reported in certain other genera, such as *Cardioneuropteris* (Goganova *et al.* 1993) and *Eusphenopteris* (Laveine 1993), and the same may also have occurred in *M. macrophylla*.

Primary rachis branches

The longest preserved fragment is 380 mm long (V.63417; Pl. 2, fig. 1; Text-fig. 2A), but is clearly incomplete. The width of the main rachis of the branch is 10 mm at the base and tapers distally to 2 mm. Although the upper part of this specimen has been subject to some taphonomic distortion, it is likely that the pinna fragment with the apical pinnule preserved represents the apex of the primary rachis branch. The primary rachis branch widths of all the other specimens investigated in this study fall within this range, except for specimen V.63415 which is 11 mm wide at its broken lower part.

The lowest part of the primary rachis branch in V.63417 appears straight, but becomes kinked where each secondary rachis is attached higher in the frond. Most of the other specimens show similar kinking of the primary rachis branches. About half-way along the V.63417 primary rachis branch, there is what appears superficially to be a pseudodichotomy of the primary rachis branch,



TEXT-FIG. 1. *Macroneuropteris macrophylla* (Brongniart) Cleal *et al.* Lower parts of frond; Radstock, Somerset, UK; upper Westphalian D. A, V.63418; possible main dichotomy of frond, although the two branches are not preserved attached. B, V.63416(a); main dichotomy of small frond, reconstructed from a bent frond fragment that lies on either side of the rock slab. C, V.63416(b); primary rachis below main dichotomy with large pinnules attached. D, V.3073; primary rachis below main dichotomy with large pinnules attached. Scale bar represents 100 mm.

but this is probably the result of taphonomic distortion (note the displacement of the secondary rachises in the upper part of this specimen). A possible overtopped branch or even dichotomy of the primary rachis branch is shown in one of the fragments on V.63419 (Pl. 3, fig. 2; Text-fig. 2B), but again it is not well enough preserved to be sure if it was an original feature (other previously published examples of such branching are by Lesquereux 1879, pl. 9, fig. 2; Kidston 1888, pl. 22, fig. 2; and Crookall 1959, pl. 40, fig. 1).

V.63416(a) (Pl. 1; Text-fig. 1B) shows that the secondary rachises are attached to the two primary rachis branches of a frond at the same distance from the main dichotomy. Consequently, the inwards facing secondary rachis tips must have met more or less in the middle of the frond. There is no evidence as to whether this arrangement persisted in the higher parts of the frond.

There is little direct evidence as to the shape of the two frond segments produced by the dichotomy of the primary rachis. Very few complete secondary rachises/pinnae have been found

attached to the primary rachis branches. Although V.63417 shows the upper end of a primary rachis branch, it is impossible from this alone to determine the form of the apex of the frond segments.

Secondary rachises

Secondary rachises are attached alternately to the primary rachis branches. The lowest secondary rachises are emitted from the outwards facing sides of the primary rachis branches. In V.63416(a) (Pl. 1; Text-fig. 1B), the lowest secondary is *c.* 60 mm above the dichotomy, although this distance was probably greater in the larger, more 'typical' fronds. The angle of attachment of the secondary rachises to the primary rachis branches appears to have been 80–90° in much of the frond, although towards the frond apex the angle became narrower: 60° in V.63414 (Pl. 3, fig. 1; Text-fig. 2D) and 53° in the specimen figured by Crookall (1959, pl. 40, fig. 1). An even more acute angle is suggested by V.63417 (Pl. 2, fig. 1; Text-fig. 2A), although this may be due to taphonomic distortion.

As mentioned above, very few complete secondary pinnae have been found attached to the primary rachis branches, the only exceptions being in V.63416(a), V.63417 and V.63419(b) (Pl. 1; Pl. 2, figs 1–2; Text-figs 1B, 2A, C). From the evidence provided by the available fragments, however, they appear to have been parallel-sided for most of their length, tapering only slightly near their position of attachment to the primary rachis branch. More marked tapering occurs in the apical part of the secondary rachises, which are terminated by a single rhomboidal apical pinnule, thus exhibiting clearly an imparipinnate configuration. The terminal pinnule often shows a lateral lobe which demonstrates the mode of differentiation of the lateral pinnules from the terminal. The longest preserved secondary rachis fragment is 250 mm long (V.63419(b); Text-fig. 2C) and, from the way the attached pinnules taper in the upper part of the fragment, was probably originally *c.* 300 mm long.

Pinnules

These are found attached to all orders of rachis, both above and below the main dichotomy. The range of pinnule morphology seen in the frond is shown in Plate 4.

The most commonly found pinnule forms of this species occur along the secondary rachises (Pl. 4, figs 1–2). They are linguaeform, subfalcate or subtriangular in shape, up to 55 mm long and 15 mm wide. They are constricted, often somewhat cordate, at the base. There is usually a distinct, subauriculate basiscopic expansion, while the lamina on the acroscopic side is markedly constricted. This gives the basal part of the pinnules a distinctly asymmetrical, decurrent appearance. The pinnules have a generally acute or sometimes obtuse apex.

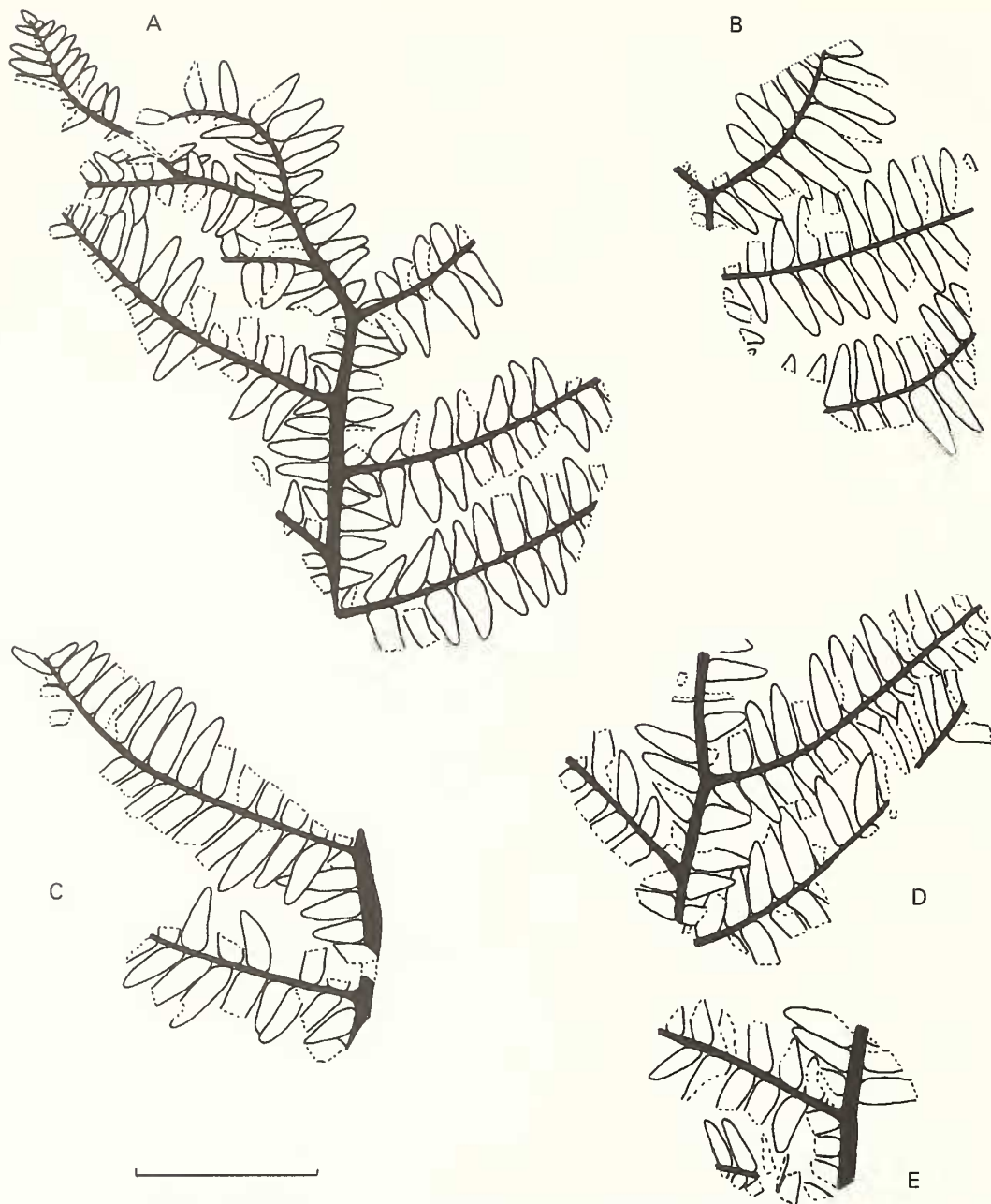
Three or four pinnules are intercalated between adjacent secondary rachises on the primary rachis branches (Pl. 4, fig. 3). They are rather similar in shape to the 'typical' pinnules described in the previous paragraph. However, the acroscopic constriction tends to be less marked in the intercalated pinnules and, in some cases, there may even be an acroscopic bulge. Moreover, adjacent to the secondary rachises, where the space available for growth is more limited, they are often squatter and more subtriangular.

V.63416(a) (Pl. 1; Pl. 4, fig. 4; Text-fig. 1B) shows that immediately below the lowest of the secondary rachises, the pinnules attached to the primary rachis branches are similar to the 'typical'

EXPLANATION OF PLATE 2

Figs 1–3. *Macroneuropteris macrophylla* (Brongniart) Cleal *et al.* Specimens photographed using cross-polarized reflected light; Radstock, Somerset, UK; upper Westphalian D. 1, V.63417; near-terminal fragment of primary rachis branch; $\times 0.5$. 2, V.63416; pinna terminal from obverse side of specimen shown in Plate 1, representing continuation of the distal-most preserved inside pinna from the right-hand primary rachis branch; $\times 1$. 3, V.3073; primary rachis below main dichotomy of frond with swollen pinnules; $\times 0.5$.





TEXT-FIG. 2. *Macroneuropteris macrophylla* (Brongniart) Cleal *et al.* Upper parts of frond, A and B showing possible pseudodichotomies; Radstock, Somerset, UK; upper Westphalian D. A, V.63417. B, V.63419(a). C, V.63419(b). D, V.63414. E, V.63415. Scale bar represents 100 mm.

pinnules attached to the secondary rachises. Approaching the main dichotomy of the frond, however, the pinnules become broader, with a subtriangular or ovoid shape. V.63416(b) and V.3073 (Pl. 1; Pl. 2, fig. 3; Text-fig. 1C–D) show that the pinnules below the main dichotomy are consistently broader and more ovoid, achieving dimensions of up to 50 mm long and 30 mm wide. There is

therefore a gradual transition between the large, ovoid pinnules attached to the primary rachis below the main dichotomy, and the more 'typical' elongate linguaeform to subfalcate intercalated pinnules higher in the frond. From this, it seems reasonable to assume that the large pinnules in the lower part of the frond lay in the same plane as the 'typical' pinnules above the main dichotomy.

The large pinnules near the base of the frond have fine, dichotomous veins radiating from their point of attachment to the rachis (Pl. 4, fig. 4). In the more elongate forms, however, there is a thick midvein along the long axis of the pinnule (Pl. 4, figs 1–2). The midvein is virtually non-decurrent in most pinnules and extends for some 90 per cent. of their length. Pinnules near the apex of the secondary rachises may have a somewhat decurrent midvein, which extends only for some of the pinnule length. Lateral veins are emitted from the midvein at a very narrow angle, and then arch broadly to meet the pinnule margin at about right-angles. The veins dichotomize three to five times, to produce a nervation density of *c.* 45 veins per 10 mm along the pinnule margin.

In no case was any evidence found of lobed (except for some terminals) or pinnatifid pinnules, forming a transition to divided pinnae. Each half of the frond produced by the major dichotomy of the primary rachis was thus essentially bipinnate.

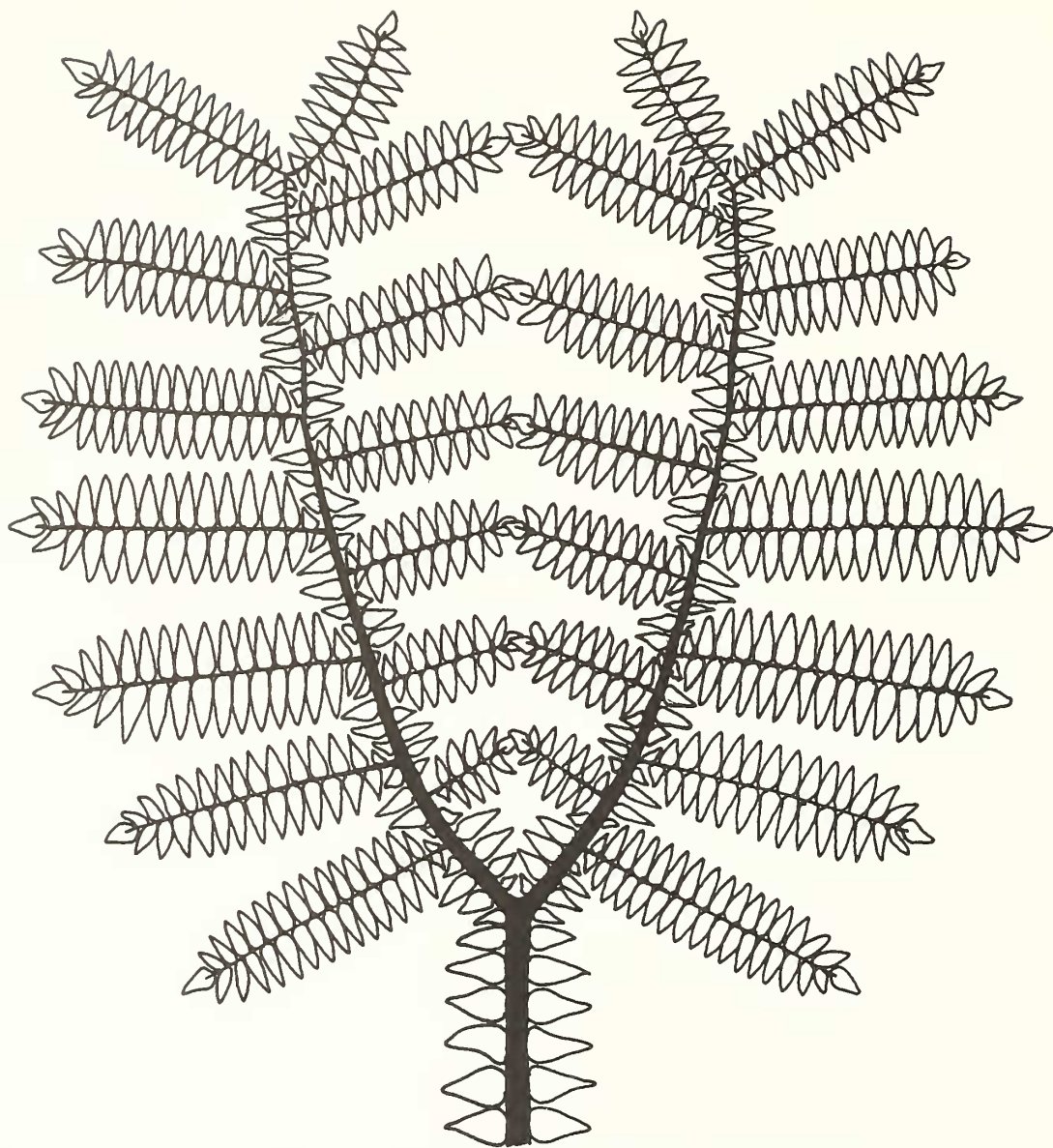
INTERPRETATION OF FROND

Our interpretation of the *Macroneuropteris macrophylla* frond is summarized in Text-figure 3. The main features of the reconstruction are fairly self-evident from the specimens: (1) an essentially bipartite architecture; (2) large, pyriform pinnules attached to the primary rachis below the main dichotomy, and more or less orientated in the same plane as the rest of the frond; (3) bipinnate primary rachis branches; (4) intercalated pinnules between the secondary rachises; and (5) pinnae terminated by single apical pinnules.

The two available specimens of *M. macrophylla* showing the main dichotomy of the frond (Pl. 1; Text-fig. 1B; Kidston 1888, pl. 21, fig. 2) show that there is a morphological gradation between the large, pyriform pinnules and the normal-shaped intercalated pinnules attached to the primary rachis branches. There is thus some comparison with the model proposed by Laveine (1967, p. 81), whereby the cyclopterid pinnules attached to the lower part of the fronds in some *Neuropteris* species (subsequently transferred to *Laveineopteris* by Cleal *et al.* 1990) also graded morphologically into normal-shaped pinnules. In contrast, using a combination of evidence from gross morphology and cuticles, Cleal *et al.* (1990) have argued that these cyclopterids of *Laveineopteris* foliage were of a fundamentally different nature to the pinnate foliage from higher in the fronds (a point of view which had also been earlier partly expressed by Potonié 1903). The status of these cyclopterids attached to *Laveineopteris* fronds remains a subject of contention, and the present authors must confess to being in some disagreement on the matter. However, they do agree that the large, pyriform pinnules of the *M. macrophylla* fronds are *not* fundamentally different from the pinnate foliage from higher in the frond, in either a functional or morphological sense.

The symmetry of the frond, with the secondary pinna tips meeting in the middle, may seem unlikely, since it results in gaps in the lamina cover in the middle of the frond; a more complete lamina cover would have resulted if the two sets of secondary pinnae were offset. We have reconstructed it in this way based on the position of attachment of the secondary rachises observed immediately above the main dichotomy. However, we recognize that there is no direct evidence of this higher in the frond, and it will have to be confirmed by more complete specimens. It is even likely that there was a probable large variation in this point.

Except for V.63416(a) and V.3073 (Pl. 1; Pl. 2, fig. 3; Text-fig. 1B, D), the dimensions of the frond fragments studied here show a remarkable consistency (see Table 1). For instance, the maximum width of the primary rachis branches in each specimen is 8–11 mm, and the secondary rachises are spaced at 90–100 mm. From this, it is assumed that most of these fragments originated from fronds of about the same size. The reconstruction that we present here is the smallest and thus simplest that can accommodate all of the available specimens, and results in a frond that is *c.* 0.8 m long from the main dichotomy to the apex (the so-called DAD dimension of Cleal and Shute 1991). Clearly,



TEXT-FIG. 3. Proposed reconstruction of an entire frond of *Macroneuropteris macrophylla* (Brongniart) Cleal *et al.* This frond would be about 1 m long.

a longer frond could be proposed, simply by extending the petiole and the primary rachis branches, and adding more secondary rachises. However, it would be expected that this would result in primary rachis branches that were wider near the main frond dichotomy.

V.63416(a) and V.3073 are smaller in most of their dimensions than the other specimens. If there is a broad correlation between these dimensions and the overall frond length, then these specimens probably originated from fronds only about half as long (DAD 0.40–0.45 m).

In the absence of more complete specimens, the overall width of the fronds is also difficult to assess. It depends mainly on the angle of the main dichotomy of the frond and the length of the

outwards-facing secondary rachises, the latter variable being unknown. The longest secondary rachis in our specimens appears to have been originally *c.* 0.3 m long, although it is not completely preserved (V.63414). By incorporating a secondary rachis of this length into our reconstruction, the frond width comes to something of the order of 1 m.

SYSTEMATIC PALAEOONTOLOGY

The suprageneric taxonomy used in this paper follows that of Meyen (1984, 1987). In particular, the original name *Trigonocarpales* is adopted in preference to the more widely used *Medullosales*, as it is linked to a form-genus of a fructification rather than of a stem. However, as there is no direct evidence of the fructifications of *Macroneuropteris*, the latter is assigned to the order as a satellite form-genus (*sensu* Meyen 1978; Thomas and Brack-Hanes 1984).

The following annotations are used in the synonymy lists following Matthews (1973), Zodrow and Cleal (1993), and Cleal and Shute (1995).

- * The protologue of the basionym.
- § The valid publication of the name accepted here.
- T The type specimen(s) when not published in the protologue, or photographic illustrations of them if the original illustrations were poor.
- ? The inclusion of this reference is provisional due, for instance, to poor illustration.
- . The present authors accept responsibility for including this in the synonymy; if a species is included as a synonym without the '·', then it is based on another authority, which is quoted at the end of the reference.
- † (Dagger-sign) for the most recent reference which includes a reasonably full synonymy and extensive illustration.
- k The reference includes cuticular evidence.
- f The reference includes frond architecture evidence.

Division GYMNOSPERMOPHYTA

Order TRIGONOCARPALES Seward, 1917, *emend.* Meyen, 1984

Satellite form-genus MACRONEUROPTERIS Cleal, Shute and Zoderow, 1990

Type. Holotype of *Macroneuropteris macrophylla* (Brongniart) Cleal, Shute and Zoderow, 1990 by original designation.

Macroneuropteris macrophylla (Brongniart) Cleal, Shute and Zoderow, 1990

Plates 1–4; Text-figures 1–3, 5

- *1831 *Nevropteris macrophylla* Brongniart, p. 235, pl. 65, fig. 1.
- .?1831 *Nevropteris acutifolia* Brongniart, p. 231, pl. 64, figs 7 [photographically refigured by Laveine 1967, pl. F, fig. 1], ?6.
- 1858 *Neuropteris Clarksoni* Lesquereux, p. 857, pl. 6, figs 1–4 [*vide* Kidston 1888].
- f1888 *Neuropteris macrophylla* Brongniart; Kidston, p. 354, pl. 21, fig. 2; pl. 22, fig. 2 (*non* fig. 3 [= *Neuropteris flexuosa* Sternberg]).
- ?1940 *Neuropteris Machadicostai* Teixeira, p. 91, pls 3–4.
- f†T1959 *Neuropteris macrophylla* Brongniart; Crookall, p. 176, pl. 38, fig. 4; pl. 39, fig. 1; pl. 40, figs 1–2 [photographic copy of Kidston 1888, pl. 22, fig. 2]; pl. 42, figs 1, 3 (*non* pl. 40, fig. 3 [copy of Kidston 1888, pl. 22, fig. 3 = *Neuropteris flexuosa* Sternberg]).
- k1989 *Neuropteris macrophylla* Brongniart; Cleal and Zoderow, p. 860, pls 104–105.
- §1990 *Macroneuropteris macrophylla* (Brongniart) Cleal *et al.*, p. 488.

Type. Holotype, by original designation, is Specimen No. 5151 of the Geological Society Collection, British Geological Survey, Keyworth, Great Britain. Provenance: Radstock Formation (upper Westphalian D), Dunkerton, near Radstock, Somerset.

Emended diagnosis. Bipartite frond, typically *c.* 1 metre long. Main dichotomy at least 190 mm from base of frond, at an angle of 65–70°, producing two bipinnate frond segments. Primary rachis

branches with a slight inward curve in their proximal part. Secondary rachises attached alternately to primary rachis branches at 80–90°. Secondary pinnae parallel-sided for most of length, tapering at their distal end and to a lesser extent in their proximal part. Pinnae terminated by a single, rhomboidal apical pinnule. Pinnules attached laterally to both primary and secondary rachises, and intercalated between secondary pinnae on primary rachis branches, and all lie in the same plane within frond. Above main frond dichotomy, pinnules typically linguaeform to subfalcate, up to 55 mm long and 15 mm wide, with more or less acute apex. Base of pinnules asymmetrically cordate, with significantly more prominent lobe on basiscopic side. Near junctions of rachises, pinnules become squatter and more subtriangular. Below main dichotomy of frond, pinnules are ovoid, up to 50 mm long and 30 mm wide. The broader, ovoid pinnules near base of frond have fine, radiating veins. In other pinnules, there is a prominent midvein, extending for much of pinnule length. Broadly arching lateral veins meet pinnule margin at about right-angles; they fork three to five times, producing nervation density of *c.* 45 veins per 10 mm on pinnule margin.

Pinnule epidermis hypostomatic; stomata brachyparacytic, with raised subsidiary cells, and polar axis orientated parallel to veins. Guard cells 20–25 μm long. Stomatal index 9–11. Adaxial epidermal cells uniformly isodiametric, up to 60 μm in size, except along midvein where they are elongate, up to 160 μm long and 50 μm wide. Abaxial epidermal cells papillate. Intercostal abaxial cells irregularly polygonal, up to 60 μm in size; costal abaxial cells more elongately subrectangular, up to 140 μm long and 30 μm wide. Multicellular file trichomes, up to 30 μm wide (length unknown), uniformly distributed over abaxial surface; none present on adaxial surface.

Comparisons and remarks on synonymy. The principal taxonomic problem concerns the synonymy with *Neuropteris clarksonii* Lesquereux, the type of which originated from Oliphant, in the Northern Anthracite Coalfield of Pennsylvania. That the two species are identical has been accepted by most European authors, on the authority of Kidston (1888), although some American palaeontologists continued to use Lesquereux's later name (e.g. Noe 1925). Bell (1938) suggested that Lesquereux's species might be given priority, due to the inadequacy of Brongniart's illustration, but this argument (doubtful anyway on strict nomenclatural grounds) is no longer acceptable following Crookall's photographic illustration of the *M. macrophylla* holotype. We accept unequivocally the synonymy of the two species. To support our view we illustrate (Pl. 3, fig. 3) a specimen from the Appalachian Coalfield, which was identified as *N. clarksonii* by a leading nineteenth-century North American palaeobotanist, R. D. Lacoe, and which agrees in all features with *M. macrophylla*.

Brongniart (1831) figured some poorly preserved specimens from the Somerset Coalfield ('near Bath') under the name *N. acutifolia*. This has been widely regarded as a later synonym of *Macroneuropteris scheuchzeri*, mainly following Bunbury (1847). Laveine (1967, pl. F, fig. 1) illustrated photographically one of Brongniart's types (his fig. 7, the specimen shown on fig. 6 cannot currently be found), and shows that it has a subtriangular pinnule with a marked subauriculate basiscopic expansion. Pinnules of this shape and with a basiscopic lobe are found very commonly in *M. macrophylla* fronds (e.g. Crookall 1959, pl. 39, fig. 1; pl. 40, fig. 1), although they also sometimes occur in *M. scheuchzeri* (e.g. Bertrand 1930, pl. 11, fig. 2). The surface of the pinnule shows one or two doubtful lines, which might be the remains of epidermal trichomes, but the

EXPLANATION OF PLATE 3

Figs 1–3. *Macroneuropteris macrophylla* (Brongniart) Cleal *et al.* 1–2, specimens photographed using cross-polarized reflected light; Radstock, Somerset, UK; upper Westphalian D. 1, V.63414; middle part of primary rachis branch showing clear development of intercalated pinnules. 2, V.63419(a); near-terminal fragment of primary rachis branch showing possible pseudodichotomy. 3, V.1976; specimen coated with ammonium chloride and photographed using plain light; Cannelton, Beaver County, north-western Pennsylvania, USA; Kittanning Coals, Allegheny Series (= Westphalian D); ultimate pinna terminal, typical of that identified by North America palaeobotanists as *Neuropteris clarksonii* Lesquereux. All $\times 0.5$.



evidence is equivocal. The evidence tends to suggest that Brongniart's figure 7 belongs to *M. macrophylla*, although one of us (JPL) has examined other, unillustrated material identified by Brongniart as *N. acutifolia*, which undoubtedly belongs to *M. scheuchzeri*.

Very similar material, from the Westphalian D of the Santa Sousa Basin in southern Portugal, was described under the name *Neuropteris machadicostae* Teixeira, 1940. Many of the specimens have large, asymmetrical pinnules with a conspicuous, subauriculate basiscopic expansion, and are almost identical to the pinnules attached to the secondary rachises of *M. macrophylla* (Pl. 4, figs 1–2). They are associated with subtriangular pinnules (Teixeira 1940, pl. 4, figs 3, 5) that can be compared directly to the shorter intercalated pinnules in *M. macrophylla* (Pl. 4, fig. 3). There is even one example of a pyriform pinnule (Teixeira 1940, pl. 3, fig. 7) that looks identical in shape to the large pinnules from below the main dichotomy of the *M. macrophylla* frond (Pl. 4, fig. 4). Teixeira regarded his material as having more elongate pinnules than *M. macrophylla*. However, this was probably because he took a specimen figured by Seward (1910, p. 569), which in fact is quite atypical in morphology, as a typical representative of the latter species. When compared with the specimens documented in the present paper, there can be seen to be little justification in not assigning these Portuguese specimens to *M. macrophylla*.

Crookall (1959) regarded *Neuropteris squarrosa* Ettingshausen, 1852, from the middle Westphalian of Czechoslovakia, as a later synonym of *M. macrophylla*. However, Němejc and Šetlík (1950) had earlier noted that the former had anastomosed veins, and referred the specimens to *Linopteris neuropteroides* (Gutbier).

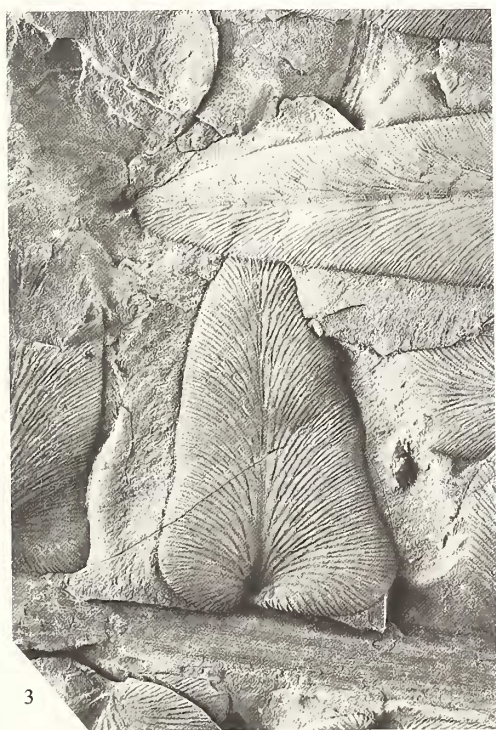
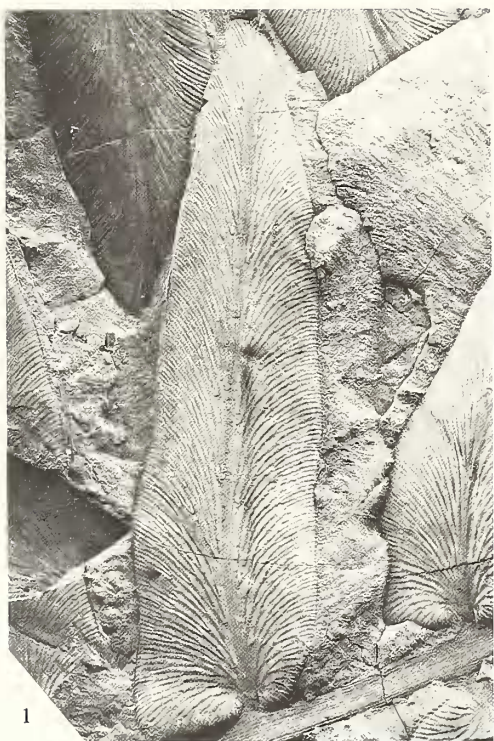
General remarks. There is no direct evidence of the fructifications or cauline anatomy of this species. Lesquereux (1880) comments that his specimens were associated with seeds 'typical of *Neuropteris*', but he does not describe or illustrate them. The species is included within the Trigonocarpaceae (Medullosales auctt.) based on the broad similarity of its frond architecture with *Neuropteris ovata* Hoffmann, which has been demonstrated to be attached to *Medullosa noei* Steidtmann axes (Beeler 1983).

Distribution. The best illustrated records of *M. macrophylla* from Europe are from the Radstock and Farrington formations, in the Bristol–Somerset Coalfield (Kidston 1888; Moore 1938; Crookall 1959). There is also unpublished evidence from the Publow Formation of the same coalfield (R. H. Wagner, pers. comm.). The only other reliable record from Europe is from the Westphalian D of the Santa Sousa Basin of Portugal. Records from the Bolsovian and Duckmantian of Britain mentioned by Crookall (1959) cannot be substantiated and probably represent misidentifications of *Macroneuropteris scheuchzeri*. The records listed by Crookall from elsewhere in Europe are over a century old and unillustrated, and must be treated with considerable suspicion.

The best documented records from North America are from the Maritime Provinces of Canada, where it has been found associated with the Harbour, Lloyd Cove and Point Aconi seams (upper Morien Group; upper Westphalian D to lower Cantabrian) of the Sydney Coalfield (Bell 1938; Zodrow 1986; Cleal and Zodrow 1989). In the rest of North America, there are well-documented records from the Northern Anthracite Coalfield, near Wilkes-Barre in north-east Pennsylvania (Lesquereux 1854, 1879, 1880). Few stratigraphical details were supplied, but the specimens probably originated from the upper Allegheny (Darrah 1969), and are thus probably of late Westphalian D or early Cantabrian age (Wagner in press). Lesquereux (1880) also described specimens from the Kittanning Coals worked at Cannelton, in the northern part of the Appalachian Coalfield. These, again, are likely to be late Westphalian D in age, although perhaps marginally older than the

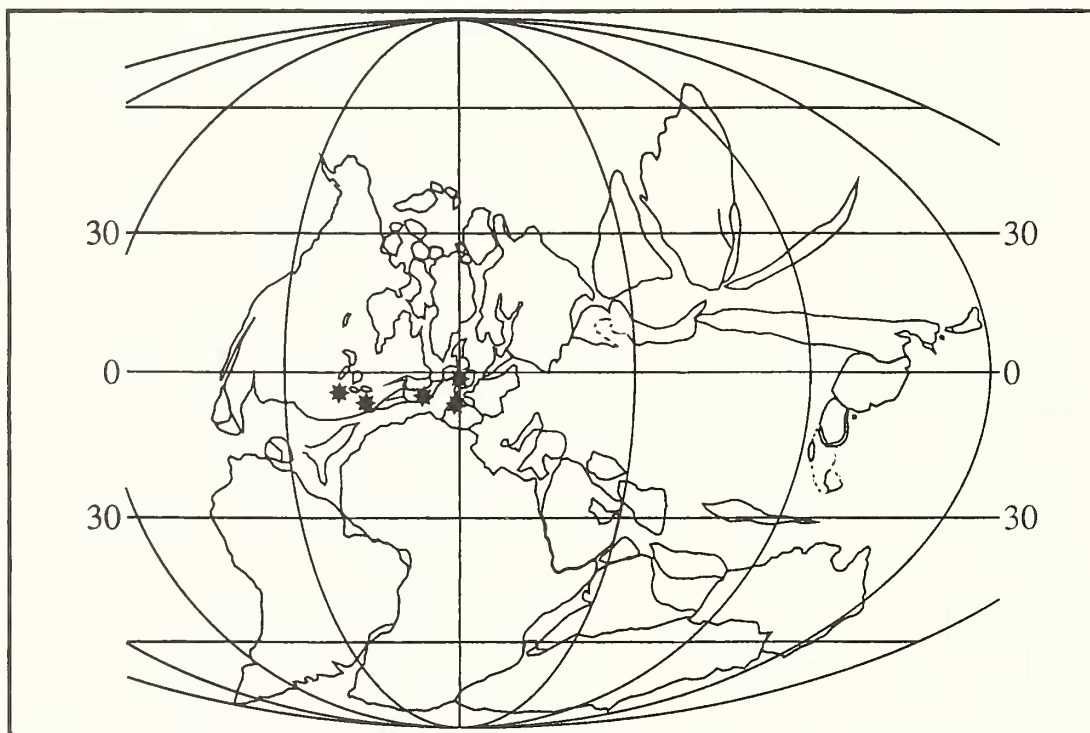
EXPLANATION OF PLATE 4

Figs 1–4. *Macroneuropteris macrophylla* (Brongniart) Cleal *et al.* Range of morphology in pinnules, photographed under ammonium chloride; Radstock, Somerset, UK; upper Westphalian D. 1, lanceolate lateral pinnule attached to secondary rachis. 2, subfalcate lateral pinnule attached to secondary rachis. 3, subtriangular, intercalated pinnule attached to primary rachis branch. 4, swollen pinnule attached to primary rachis, below main dichotomy of frond. 1–3, V.63414; 4, V.63416(b). All $\times 2$.





TEXT-FIG. 4. *Macroneuropteris scheuchzeri* (Hoffmann) Cleal *et al.* V.63894; close-up of typical pinnules showing epidermal hairs, photographed under plane-polarized light; Radstock, Somerset, UK; upper Westphalian D; $\times 2$.



TEXT-FIG. 5. Geographical distribution of *Macroneuropteris macrophylla* (Brongniart) Cleal *et al.*, plotted on a Late Carboniferous base map from Thomas and Cleal (1993, p. 5), originally adapted from Laveine *et al.* (1993).

specimens from the Northern Anthracite Coalfield (Darrah 1969; Pfefferkorn and Gillespie 1980). White (1900) gave an unillustrated record of this species from the Southern Anthracite Coalfield of Pennsylvania, from strata equivalent to or marginally older than the Cannelton occurrences.

Darrah (1969) argued that records of this species from Mazon Creek in fact refer to *Neuropteris decipiens* Lesquereux. The latter is an equivocal species, very similar to *Macroneuropteris scheuchzeri* except in the apparently larger size of the pinnules.

From outside of the eastern belt of US coalfields, there are records of this species from the Western Interior Coalfield of Missouri (White 1893) and Kansas (Sellards 1908; Cridland *et al.* 1963). Sellards' specimens originated from the Canabiss Formation, and are approximately coeval with the Wilkes-Barre material, but Cridland *et al.* dismissed them as misidentified specimens of *Macroneuropteris scheuchzeri*. The material identified by Cridland *et al.* as *N. clarksonii* (i.e. *M. macrophylla*) originated from a higher stratigraphical horizon, in the Missourian (?Stephanian B). The specimens have subtriangular pinnules with a narrowly acute apex, and many show a clear proximal curvature. They are thus quite different from the typical form of *M. macrophylla* and are more similar to the specimens figured by Cridland *et al.* as *Neuropteris hastata* White.

M. macrophylla thus appears to be restricted to a narrow area of westernmost Europe and eastern North America, which in most Late Carboniferous palaeogeographies are shown to be close together (Text-fig. 5). However, this restricted distribution may also reflect stratigraphical factors. The Somerset Coalfield is one of the few northern European paralic coalfields to range up into the upper Westphalian D and it is possible that the *M. macrophylla*-bearing plant existed in some other paralic coal basins, whose sequences have been removed by subsequent erosion. On the other hand, there are some areas where sequences of this age are preserved (e.g. South Wales, Forest of Dean, English Midlands) and where unequivocal evidence of *M. macrophylla* has not been found. Similarly, well known upper Westphalian D sequences in Saar-Lorraine, Bohemia, Ukraine and northern Spain have all failed to yield this species.

DISCUSSION

Is Macroneuropteris a natural genus?

The frond architecture data provided in this paper, together with the cuticle evidence described by Cleal and Zodrow (1989), may be taken as providing the essence of *Macroneuropteris* Cleal *et al.*, 1990. *M. scheuchzeri* (Hoffmann) was also included by Cleal *et al.* in this form-genus, based partly on the cuticle evidence presented by Gothan (1915), Barthel (1961) and Cleal and Zodrow (1989). Some preliminary observations on the frond architecture of *M. scheuchzeri* have been made by Laveine (1967) and Laveine and Brousmiche (1982), but more complete material from Nord-Pas-de-Calais is now available and is currently being investigated. The initial results of this study appear to confirm that the architecture of the *M. scheuchzeri* frond has many features in common with that of *M. macrophylla*. For the other two species included by Cleal *et al.* (1990) in *Macroneuropteris* (*M. britannica* (Gutbier) and *M. subauriculata* (Sterzel)), no large frond segments have been documented in the literature and so their frond architecture is poorly understood; the revision of their generic position was proposed almost exclusively on cuticular evidence. In view of the importance that Cleal *et al.* (1990) and Cleal and Shute (1991) have placed on integrating gross morphology and cuticular evidence for establishing a robust taxonomy for these fronds, the systematic position of these two species must be regarded as questionable.

Are *M. scheuchzeri* and *M. macrophylla* closely related phylogenetically or is the morphological similarity merely an analogous solution to a common problem of adaptation? Neither species has yielded evidence of fructifications or rachis/stem anatomy. Nor is there any direct evidence of a gradation between the two species through time, as has for instance been demonstrated between *Neuropteris obliqua* (Brongniart) Zeiller and *Reticulopteris muensteri* (Eichwald) Gothan (Josten 1962; see also Zodrow and Cleal 1993; Cleal and Shute 1995). *M. macrophylla* must have evolved in habitats not represented in the fossil record, and that record can therefore provide no direct evidence of its ancestors. All that can be said is that both species share many features of morphology and epidermal structure, and that the balance of evidence tends to suggest that they represent a natural genus.

Macroneuropteris and Neuropteris compared and contrasted

Macroneuropteris is most similar to *Neuropteris*, as reconstructed by Zodrow and Cleal (1988) and Cleal and Shute (1991). The general architecture is identical, except that *Neuropteris* fronds are more divided (the primary pinna branches are at least tripinnate, instead of essentially bipinnate in *Macroneuropteris*). The pinnules of *M. macrophylla* are thus homologous with the segmented

tertiary pinnae of *Neuropteris* (Laveine 1967, p. 68; Laveine 1989, p. 44). The homology is confirmed in *M. scheuchzeri*, in which the pinnules often develop basal lobes, and thus could be interpreted as being transitional to tertiary pinnae. It is quite clear that the underlying frond architecture of the two frond-types is very similar and that they are almost certainly closely related. Following the arguments advanced by Laveine (1967), this might indicate that *Macroneuropteris* is merely a retarded growth form of typical neuropterid fronds. However, *Macroneuropteris* fronds were probably not significantly smaller than those of *Neuropteris heterophylla* (Laveine 1967; Cleal and Shute 1991). It also ignores the differences in epidermal structure, which Cleal *et al.* (1990) used as additional support for separating *Macroneuropteris* from *Neuropteris*.

Typical neuropterids often show a broad transitional zone in the upper and sometimes the lower regions of pinnae, where pinnules are changing to pinnae (e.g. Crookall 1959, pl. 26; Laveine 1967, pl. A, fig. 1c; Cleal and Shute 1991, figs 2–8). This is less pronounced in *Macroneuropteris*, and in *M. macrophylla* totally absent. In *M. scheuchzeri*, it is limited to the development of pinnae with one (anadromic) pinnule (usually designated as a lobe), then two (one anadromic and one catadromic) pinnules and, very exceptionally (on the primary rachis branches) three (two anadromic and one catadromic) pinnules. Some evidence of a transitional zone between pinnule and pinna is also offered by the '*Odontopteris lindleyana*' specimens illustrated in Laveine (1967, pl. 69, fig. 4, 4a) and Darrah (1969, pl. 26, fig. 3; pl. 34, figs 2–3; pl. 62, fig. 4). However, there is no direct evidence as to where such lobed pinnules occur in the frond, and so their morphological significance is not certain.

As *Macroneuropteris* has so many features in common with *Neuropteris* and the two are probably closely related, what is the justification for maintaining the generic distinction proposed by Cleal *et al.* (1990)? Laveine (1967, p. 314), while recognizing the distinctive morphology of the *Neuropteris* 'macrophylliens' species, argued that separating them in a new genus risked misleading non-specialists as to their natural relationship with *Neuropteris*. Whether or not this view is accepted probably depends to an extent on whether one is a 'lumper' or a 'splitter'. It must also be stated that Laveine's original view was based purely on gross morphology, as very little epidermal evidence had at that time been published, and the northern French fossils on which Laveine was then working do not yield cuticles. Cleal *et al.* (1990), when proposing the separation of the two genera, emphasized that it was based on an integration of cuticular and gross morphological evidence. It has also been found from a distributional analysis of neuropteroids in Europe (Cleal and Shute 1995), that species of *Neuropteris sensu* Cleal *et al.* (1990) and of *Macroneuropteris* appear to show different patterns of diversity, suggesting that they represent the foliar remains of separate groups of plants, probably sharing a common ancestry, but which reacted differently to environmental (e.g. edaphic) changes. Despite this, it is still clearly a subjective decision as to whether two groups of frond-types are separated generically; whether the separation continues to be maintained will depend on whether palaeobotanists find it useful for expressing their phylogenetic or distributional ideas.

Comparison of Macroneuropteris with other neuropteroid fronds

Laveineopteris is similar in most gross morphological characters to *Neuropteris*, except for the presence of large cyclopterid pinnules near the base of the frond. These cyclopterids are single pinnules attached directly to the primary rachis or primary rachis branches, and thus might appear comparable to the large ovoid pinnules attached to the primary rachis of *M. macrophylla*. However, these pinnules in *M. macrophylla* appear to be homologous to the pinnate foliage above the main dichotomy, being arranged in the same plane, and there being a gradational morphological series between them. In contrast, the cyclopterids of *Laveineopteris* have a quite different epidermal structure from the pinnate foliage (Cleal and Zodrow 1989). Furthermore, the larger laveineopterid cyclopterids in particular do not appear to have been originally orientated in the same plane as the rest of the frond, a feature that is shown by all of the larger specimens showing attached cyclopterids (von Roehl 1868, pl. 17; Carpentier 1930, pl. 8; Gothan 1953, text-fig. 8; Laveine 1967, pl. O,

fig. 1; pl. 45, fig. 3). Also, the strongly cordate base of many of these cyclopterids (e.g. Crookall 1959, pl. 27, fig. 7) is more compatible with them having originally been wrapped partially around the primary rachis. Unfortunately, there is no cuticular evidence for these large *M. macrophylla* pinnules, but their orientation and their gradation into normal-shaped pinnules suggests that they are not cyclopterids in the sense of Cleal and Zodrow (1989) and Cleal *et al.* (1990).

Certain specimens of *Macroneuropteris* (e.g. Text-fig. 2D; Crookall 1959, pl. 40, fig. 1) can appear very similar to *Paripteris* (e.g. Laveine 1967, pl. 71, fig. 2), such that the two genera might be thought to be synonymous. This is particularly suggested by the presence of intercalated pinnules on the penultimate rachises. It would be easy to believe that the pinnules are homologous structures in the two genera. However, the overall architecture of the fronds is fundamentally different (Laveine 1967, p. 68), most significantly in that the *Macroneuropteris* pinnae are imparipinnate (i.e. have just one apical pinnule), whereas *Paripteris* is paripinnate (i.e. pinnae have a pair of apical pinnules). Furthermore, *Paripteris* fronds never have lobate pinnules (Laveine 1967, pp. 247, 250; Laveine *et al.* 1993). It is true that neither does *M. macrophylla*, but the slightly more divided *M. scheuchzeri* frond shows the start of pinnule lobing by the development of one, two or, very rarely, three lobes (or incipient pinnules) at their base. This all reflects a major difference in the mode of frond construction for *Paripteris*, in which different orders of segmentation of the frond are produced exclusively by dichotomies and overtopping of the rachises, a construction that has been termed 'pseudo-pinnate' (Laveine *et al.* 1993), and suggests that *Paripteris* and its anastomosed veined counterpart *Linopteris* are only very distantly related to *Macroneuropteris*.

Using Macroneuropteris to understand the Neuropteris frond

The 'simplified' frond architecture of *M. macrophylla* can help in understanding the apparently more complex architecture of *Neuropteris* and *Laveineopteris* fronds. The reconstruction of the *M. macrophylla* frond shown in Text-figure 4 may be interpreted as follows. A primary rachis, bearing large pinnules, bifurcated to produce two equal primary rachis branches. Each of the primary rachis branches underwent a series of overtopped bifurcations, producing lateral ramifications (external and internal), organized and developed according to the available space within the frond. That the secondary pinnae are the product of overtopped dichotomies and were not merely produced by increasing the segmentation of the intercalated pinnules near the main dichotomy is clearly shown by specimen V.63416(a) (Pl. 1; Text-fig. 1B). If the frond was built only by a progressive increase in the differentiation of the laminar elements, then one should find, moving up from the dichotomy in this specimen, a gradation between the lowest, simple, entire pinnule and the first internal secondary pinna. This is obviously not the case and, in fact, the pinnules become slightly smaller near the first internal secondary pinna. The secondary pinnae must be the product of overtopped dichotomies and not a simple lateral mode of branching. The distal parts of the primary rachis branches in specimens V.63419(a) and V.63417 (Pl. 2, fig. 1; Pl. 3, fig. 2; Text-fig. 2A–B) also clearly show a more or less dichotomous, overtopped manner of branching.

By increasing the division of the secondary segments, it is possible to use this model to understand the construction of the *Neuropteris* fronds, as follows. A primary rachis, bearing ultimate pinnae (or possibly their homologous equivalents), bifurcated to produce two equal primary rachis branches. Each of the primary rachis branches underwent a series of overtopped bifurcations producing lateral ramifications (e.g. Laveine *et al.* 1977, text-fig. 6; Cleal and Shute 1991, fig. 2). These lateral ramifications appeared first on the external (catadromic) side of the primary rachis branches, where there was no special problem of available space. Inside the main dichotomy, the most proximal elements are ultimate pinnae, becoming progressively longer away from the main dichotomy as more space became available. However, these are not the products of overtopped branching, but merely the equivalent of the intercalated pinnae on the outwards facing side of the primary rachis branches (i.e. homologues of pinnules in the *M. macrophylla* frond). This is indicated by the absence of any intercalated foliar elements (which would presumably in this case be small lobate pinnules) between these most proximal, inwards facing pinnae on the *Neuropteris* frond. Only at a much more

distal position in the frond, when space became less of a problem in the centre of the frond, did overtopped branching occur to produce inwards-facing secondary pinnae, these being recognizable by the presence of short pinnae intercalated between them.

This general model appears to be further supported by the only known specimen of *Neuropteris guardinis* Grand'Eury (1890, pl. 22, fig. 2) as interpreted by Laveine (1967, text-fig. 14). The same mode prevails for the frond of *Odontopteris*, although because they were smaller, the overtopped dichotomies only produced secondary pinnae on the external side, the space available on the internal side having been too restricted.

Acknowledgements. We thank the Photographic Studio of The Natural History Museum, London, for photographing the specimens illustrated in this paper.

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Typescript received 16 January 1995
Revised typescript received 11 August 1995

NOTE ADDED IN PROOF

One of us (CJC) has recently been shown a specimen (SM X.27508) in the collections of the Sedgwick Museum, Cambridge, that clearly demonstrates overtopped branching in the distal part of a *M. macrophylla* primary rachis branch. This, therefore, confirms the reconstruction of this part of the frond given in Text-figure 3. This specimen will be documented in a later publication.